AMERICAN MUSEUM NOVITATES

Number 577 — Published by THE AMERICAN MUSEUM OF NATURAL HISTORY New York City — Nov. 4, 1932

56.9, 71 C (1181:82.9)

COCHILIUS VOLVENS FROM THE *COLPODON* BEDS OF PATAGONIA[1]

By GEORGE GAYLORD SIMPSON

In the collection made by the Scarritt Patagonian Expedition in the *Colpodon* Beds south of Lago Colhué-Huapí are a number of fine specimens of *Cochilius volvens* revealing all of the skull and dentition and part of the skeleton. This genus is a very interesting one and has never been figured or described in any detail.

In the present paper its anatomy is illustrated and briefly described and its affinities discussed. The drawings are by John C. Germann.

MATERIAL

The principal specimens here considered are listed below. All are from the same locality, that south of Colhué-Huapí whence came Ameghino's best specimens of this fauna, and within a few feet of the same horizon. Although somewhat variable, all these specimens are referred to *Cochilius volvens*. Ameghino named two other species, both poorly known and both larger than any of these specimens.

Amer. Mus. No. 29651, complete, well preserved skull with dentition complete except I^{2-3} right and I^3–C left.

Amer. Mus. No. 29686, lower jaw with partial dentition, right humerus, radius, ulna, and part of manus, many vertebræ and ribs.

Amer. Mus. No. 29652, lower jaw nearly complete, with right P_2–M_3 and left I_{2-3}, P_1–M_3.

Amer. Mus. No. 29653, left lower jaw with P_1–M_3.

Amer. Mus. No. 29658, right lower jaw with I_1–C, P_2–M_3.

Amer. Mus. No. 29654, right lower jaw with I_1–C, P_3–M_3, and left I_1.

Amer. Mus. No. 29655, part of rostrum and palate with right I^1–M^1 and left I^{1-2}.

Amer. Mus. No. 29657, part of right maxilla with P^1 or dm^1, unerupted P^{2-3}, dm^4, and M^{1-3}.

MORPHOLOGY

Cochilius will be described chiefly by comparison with its closest relatives in the Santa Cruz, *Protypotherium* and *Interatherium*, both already well described by Sinclair.

DENTITION.—The median upper incisors are quite as much enlarged as in *Protypotherium australe*, in some cases even a little more, but have

[1]Publications of the Scarritt Patagonian Expedition, No. 9.

distinctly lower crowns. On all the incisors and also on the canine the enamel is confined to the labial surface in the worn specimens available. These teeth all have closed roots. I^1 is scalpriform, slightly heavier near the midline. I^{2-3} are subequal, smaller than I^1 and similar in form but still more asymmetrical, heavier anteriorly. The three incisors and the canine imbricate, their thinner posterior edges lapping outside the following tooth. The canine is smaller than any of the incisors and similar in form except that it rises to a more definite anterior cusp, perhaps the effect of different and less severe wear. Unlike that of *Protypotherium australe*, it is not grooved externally. There is little or no cement on these anterior teeth. They resemble *Protypotherium* in the absence of diastemata and better development of the lateral incisors and canines than in *Interatherium*.

P^1 is a small tooth, about as long (anteroposteriorly) as the canine but wider transversely, although the length still exceeds the width. The inner face is incompletely enamel-covered, unlike the following teeth which have internal enamel at all stages of wear, or the preceding ones which have it only at the apex if at all. This tooth probably forms a closed root. The molars and posterior premolars have open roots at least until an advanced age and perhaps throughout life, but the exact point of division in the dentition between this and the rooted condition is not established. In the lower jaw P_1 certainly and P_2 probably form closed roots. In the two Santa Cruz genera all the cheek teeth are rootless. P^1 may have the internal face simply convex (Amer. Mus. No. 29655) or with a shallow vertical groove (Amer. Mus. No. 29651), probably an age character. The outer face is flattened and has a small ridge at the anterior angle.

Save for their progressive increase in size, P^{2-4} are closely similar. There is a strong sulcus on the internal face, which shows some tendency to bifurcate. This sulcus divides the face into two nearly equal lobes as in *Interatherium*, whereas in *Protypotherium* the sulcus is generally near the anterior edge and the lobes decidedly unequal. As a result, these teeth are distinctly more molariform in the earlier genus and in *Interatherium*, although this does not necessarily make them more advanced in this respect, as the condition in *Protypotherium* could well be a specialization, or at least there is no warrant for considering it as a retained ancestral structure. The outer faces of P^{2-4} are flattened, with a poorly defined swelling on the posterior two-thirds and two more sharply defined vertical ridges on the anterior third, between which is a narrow groove. In one specimen (No. 29651) this penetrates deeply into the anterior lobe

as a closed enamel fold, but on another (29655) it penetrates much less. It is probable that this is due to degree of wear.

M^{1-3} are similar to P^{2-4} save that the ridging and grooving of the outer wall are less strong. The anterior groove in no case penetrates the crown and may be very faint or apparently absent. M^3 does not have the posterior extension or incipient third lobe seen in some specimens of *Protypotherium*. On all the cheek teeth (save P^1) the sculpturing of the outer wall resembles the latter genus and is much weaker than in *Interatherium*.

I_{1-2} occlude against the large I^1. I_{1-3} are progressively larger and of rather similar form, between styliform and spatulate and distinctly bilobed on the inner surface when little worn. The roots are long but closed; the crowns, completely invested in enamel, are high but less so than in the Santa Cruz genera. The canine is almost identical in form

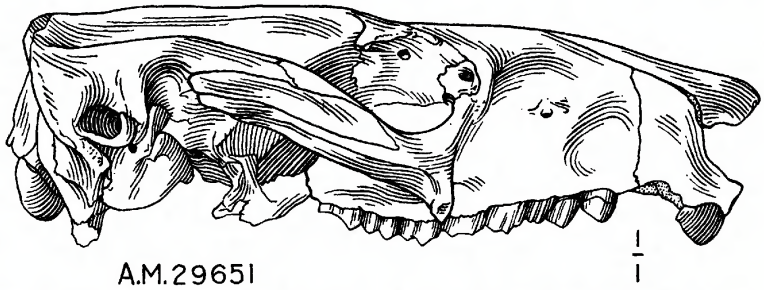

Fig. 1.—*Cochilius volvens* Ameghino. Amer. Mus. No. 29651. Skull, right lateral view. Natural size.

with the incisors but with a very slight posterior basal expansion, and P_1 also differs very little but has a more distinct posterior and slight anterior blade-like extension.

P_2 has much the same form as the following teeth when deeply worn except for its relatively greater length and lesser width, but when unworn, as it is in No. 29652, it shows in a clear and interesting way the origin of this columnar pattern from the basic molar form underlying the whole great notoungulate group. It is lophiodont, divided into trigonid and talonid crescents perfectly united at the metaconid, which is the highest cusp. Within the talonid crescent is the transverse entoconid crest, united nearly to its apex with the middle of the crescentic hypoconid-hypoconulid crest. The external sulcus between the hypoconid and protoconid and the internal sulcus between the entoconid and the metaconid persist on all the teeth throughout life and define the two

prisms of the worn teeth. The anterointernal groove, in the trigonid crescent, disappears rapidly with wear. The postero-internal groove, between the entoconid and the hypoconulid, persists longer and is present as a deep narrow sulcus on some worn premolars, but eventually it, too, disappears and there is no trace of it on any of the molars preserved.

As with the upper premolars, the lower premolars are more molariform in *Cochilius* than in *Protypotherium* and except for P_1 closely resemble those of *Interatherium*. The two prisms are nearly equal on P_{2-4}, or the posterior slightly larger on P_4. In *Protypotherium* the posterior lobe is considerably smaller on all three.

Lower molars and posterior premolars consist of two prisms united by a narrow isthmus internal to the midline. Each lobe is rounded on the

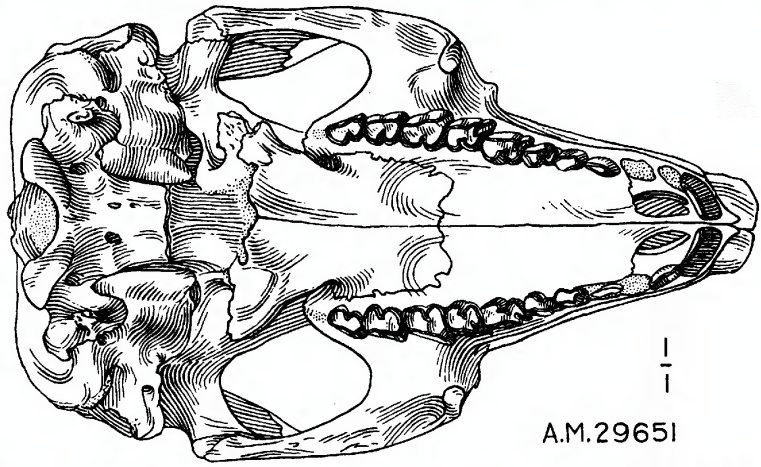

Fig. 2.—*Cochilius volvens* Ameghino. Amer. Mus. No. 29651. Skull, palatal view. Natural size.

outer side and more flattened on the inner. The longer posterior lobe is slightly and evenly convex internally, and the anterior lobe has a small, well-defined posterior vertical crest. The posterior prism of M_3 is elongate, with very shallow external and internal grooves vaguely tending to cut off a third lobe.

Amer. Mus. No. 29657 had the milk teeth still in place, although M^3 is already well worn, such late replacement being common in typotheres. P^1 of this specimen is a rooted tooth already in use but apparently without a successor, so that it is doubtful whether this is really P^1 or dm^1 and whether there was a replacement here. P^{2-3}, not yet erupted, have the grinding surface deeply covered with cement, beneath which is a thin, apparently complete enamel coating.

SKULL.—The premaxilla resembles that of *Interatherium* more than that of *Protypotherium*. It is shorter than in the latter and has no ascending process between the maxilla and the nasal. The suture against the maxilla is a simple vertical line. It reaches the alveolar border at the middle of I^3, but this tooth is wholly implanted in the premaxilla, the posterior part of the alveolus being surrounded by a thin wall from that bone which is mortised into the maxilla. The maxilla is also nearly like that of *Interatherium*. The superior process, set into the frontal above the orbit, is stouter than in *Protypotherium* and a little longer than in *Interatherium*. The descending process below the orbit on the base of the zygoma is much stronger than in *Protypotherium* but slightly shorter

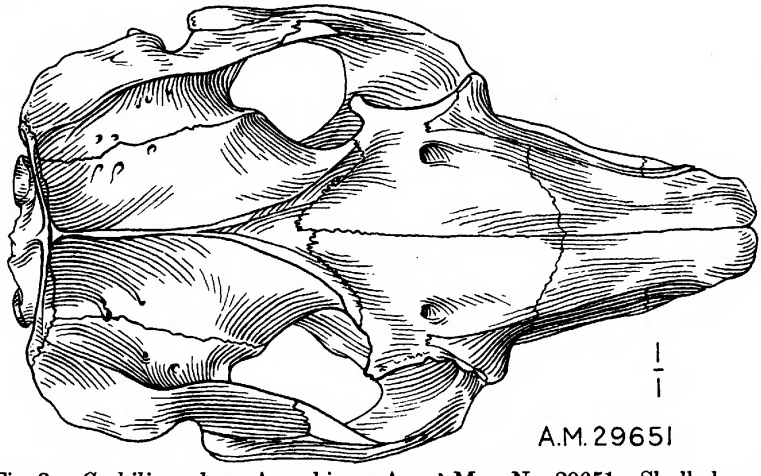

Fig. 3.—*Cochilius volvens* Ameghino. Amer. Mus. No. 29651. Skull, dorsal view. Natural size.

than in *Interatherium*. The facial part differs from that of either of the later genera in having not a single broad concavity, but two, the more anterior one smaller, deeper, and more definite.

The fronto-nasal suture, often highly variable in this family, is an even curve, convex forward. The postorbital processes are well developed, as in *Protypotherium*. The sagittal and lambdoid crests are nearly as in *Interatherium*, differing from *Protypotherium* chiefly in the greater transverse length of the latter, with which is related the lesser divergence of the opposite squamoso-parietal sutures.

The curious zygoma is nearly the same in all three genera, and is essentially formed by maxilla and squamosal. The jugal is a thin splint of bone, excluded from the orbital rim and not appearing on the inner

surface of the zygoma at all except at its posterior end. Here the jugal above and the end of the maxilla below form a vertical wall at the outer side of the glenoid surface.

The occiput has about the proportions of *Interatherium*, broader and lower than in *Protypotherium*, and the paroccipital processes are much shorter and stouter than in the latter genus. The epitympanic sinus is only slightly cancellous, apparently less so than in either of the Santa Cruz genera.

Save for minor differences in variable details of proportions or sutures, the lateral wall of the cranium is constructed as in *Protypotherium* as described by Sinclair. The basicranium is relatively shorter and broader than in *Protypotherium* but in general agreement except that the basioccipital has no keel, that in this apparently fully adult specimen

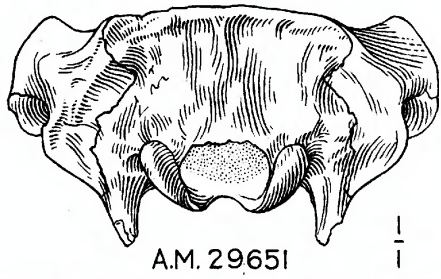

Fig. 4.—*Cochilius volvens* Ameghino. Amer. Mus. No. 29651. Skull, occipital view. Natural size.

all sutures are still open and the bullæ not fused with surrounding elements, and that the basisphenoid is pierced by two prominent vascular foramina.

The posterior margin of the palate is about as in *Protypotherium*, but with the posterolateral notches even more deeply incised.

In its general proportions the skull resembles *Interatherium* in being broad and low and *Protypotherium* in the greater development of the rostrum and median position of the orbits.

The lower jaw differs considerably from *Interatherium* and is very like that of *Protypotherium* but has some features of special interest. As in this whole family and some other typotheres, the angle projects backward well beyond the condyle. The bone is very thin. On the outer side of the base of the coronoid, below and anterior to the condyle, is an indefinitely bounded shallow depression. The insertion of the masseter below this is not really a fossa, but plane or even gently convex. Its lower and posterior margin is sharply marked by a rugose line. Below

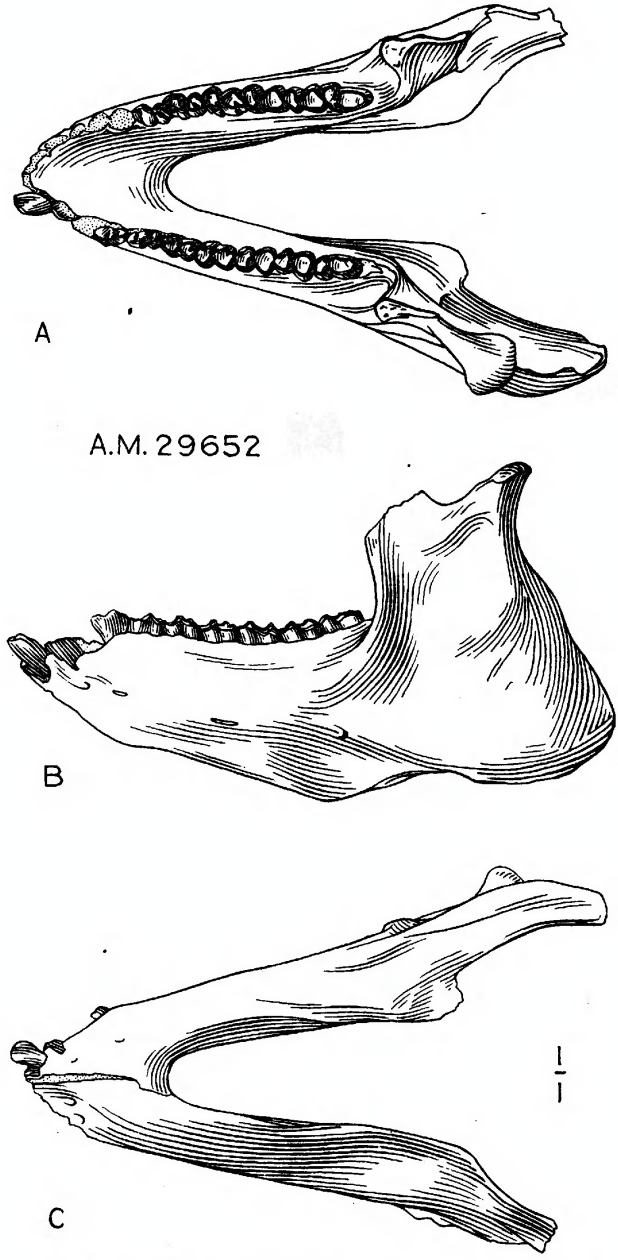

Fig. 5.—*Cochilius volvens* Ameghino. Amer. Mus. No. 29652. Lower jaw. A, Superior view. B, Left lateral view. C, Inferior view. Natural size.

and behind this the thin bony margin is inflected. In this whole family, the inferior margin of the jaw is expanded into a thin flange below the posterior cheek teeth and anterior part of the coronoid. In *Interatherium* this extends straight downward and forms what almost appears to be a second, more anterior angular process which has a homologue or analogue in some other groups, as for instance, in *Urocyon* among canids. In *Protypotherium* the anterior part of this flange is vertical, but the posterior part is somewhat inflected. The condition is almost exactly similar in some specimens of *Cochilius volvens*. On the right side of Amer. Mus. No. 29652, the process is unusually well developed but has this same character. On the left side of the same individual, the posterior part of the inflected flange extends inward and backward in a definite angular process, separated by a notch from the less inflected inferior mandibular border behind it.

In both *Interatherium* and *Protypotherium* a deep groove leads into the dental foramen from above. In both of the two specimens of *Cochilius volvens* that show it completely, this has undergone a striking further development. At a distance of 1.5 to 3 mm. from the dental foramen the groove enters the jaw through a separate foramen, communicating internally with the dental canal. In another specimen the bridge of bone separating the two foramina seems to have been absent, but the specimen is not perfectly preserved and some doubt remains. The character was probably variable.

As in the later genera, there are, with fair constancy, one small posterior mental foramen below or near P_4 and two anterior mental foramina near I_3 and C.

Fore Limb.—The fore limb is very closely similar to that of *Interatherium* except in a few details. It is more slender throughout, even a little more slender than in *Protypotherium*. The humerus is somewhat crushed but probably had as an original feature a narrower trochlea and certainly had a very sharp and prominent inner crest. As in *Interatherium* and strikingly unlike *Protypotherium*, there is no trace of an entepicondylar foramen. The radius and ulna are likewise slender and the sigmoid notch deeper and more constricted than in the Santa Cruz genera, but otherwise in agreement with the latter, as is the carpus. The proximal ends of the metacarpals show less overlap in *Cochilius*. The fifth is slightly shorter relatively than in *Interatherium robustum* and all are much more elongate and slender than in that genus generally.

Parts of at least fourteen vertebræ and some other fragments are also present in Amer. Mus. No. 29686, but they reveal nothing of particular interest.

AFFINITIES

Cochilius is clearly a typothere of the family Interatheriidæ (or Protypotheriidæ). This group is characterized in the dentition by the complete (or nearly complete) dental formula, median upper incisors rooted and only moderately enlarged, lower incisors not enlarged, molars and some or all premolars rootless, upper molars with single internal sulcus simple or weakly bifurcated. The most obvious distinction in the skull is the reduction of the jugal to a thin bone overlying the maxilla and squamosal and lacking much of reaching the lacrymal. The skeleton

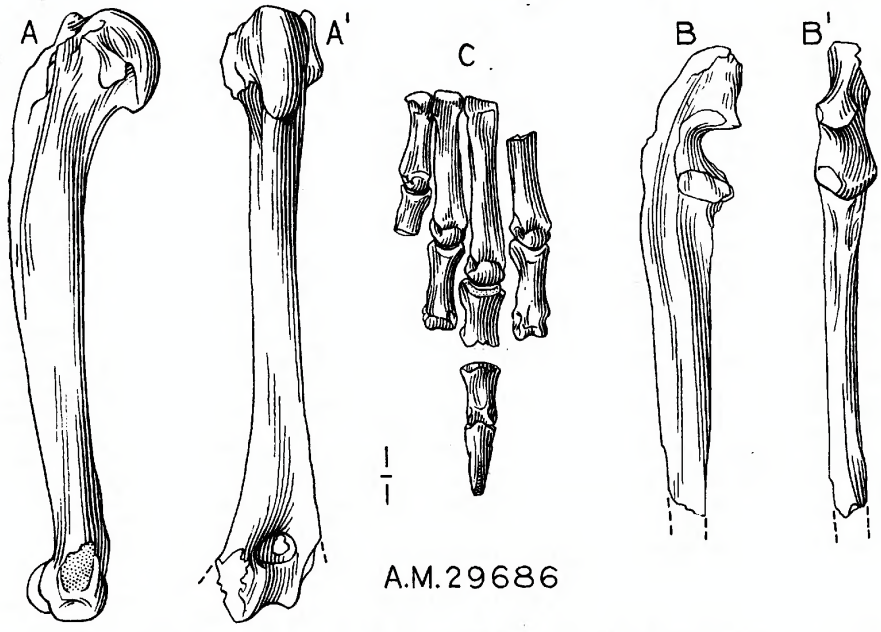

Fig. 6.—*Cochilius volvens* Ameghino. Amer. Mus. No. 29686. A, Right humerus, lateral view. A^1, Same, posterior view. B, Right ulna, lateral view. B^1, Same, anterior view. C, Right manus, dorsal view. Natural size.

is also characteristic, most strikingly so in the pes which is paraxonic, with symmetrical astragalar trochlea, and no naviculo-calcaneal facet. These distinctions, as established by Sinclair, characterize two Santa Cruz genera, *Protypotherium* and *Interatherium*. So far as comparable parts are known, they are also present in *Cochilius* which thus enters into this family.

Its resemblance to the Santa Cruz genera is not confined to primitive characters, the retention of which is one of the outstanding features

of the family, but extends also to various specializations, so that *Cochilius* cannot be very near the exact ancestry of genera placed in any other family.

The family lingered on into the Pliocene, for rather poorly known *Protypotherium*-like forms are found in various late Santa Cruz and post-Santa Cruz deposits, as at Monte Hermoso, but these survivors are not here of special concern.[1] The brachyodont to mesodont typotheres of the *Notostylops* beds are ancestral in a general way but none shows close special resemblance to this family. The *Pyrotherium* Beds to Santa Cruz forms are those of more immediate interest in connection with *Cochilius*. In addition to one or two genera either synonymous or too poorly known to be placed with any assurance, Ameghino named the following genera:

Santa Cruz { *Protypotherium*
Interatherium

Colpodon Beds—*Cochilius*

Pyrotherium Beds { *Archæophylus*
Plagiarthrus (+*Argyrohyrax*)

These are all very closely related, but do not represent a single progressive phylum.

The distinction between *Archæophylus* and *Cochilius* is by no means clear. In defining *Archæophylus*, Ameghino gave numerous characters, many of family value and not distinguishing the genera from any other of the four listed, others clearly of not more than specific value. The only character given by him which appears to me of possible generic value is the supposedly rooted character of all the premolars. In *Cochilius*, at least $P\frac{3}{3}$-$\frac{4}{4}$ seem to be rootless and in the Santa Cruz all the premolars are of continuous growth. This observation requires confirmation, as the deciduous molars persist well after the animal is adult and are very difficult to distinguish from permanent teeth.[2] *Archæophylus* is certainly very close to *Cochilius*, and perhaps synonymous. I have elsewhere (Simpson, 1932, p. 4) described another species probably from the *Pyrotherium* beds, *Cochilius fumensis*, that appears to be very close to the later genus in every respect and must be referred to it. If the genera are synonymous, *Archæophylus* has priority, but they may both be retained until *Archæophylus* is better known.

[1] In fact, the genotype of *Protypotherium* is from the Entrerian. Kraglievich (1931) has recently described from the same beds a new genus, *Muñizia*, with *Protypotherium*-like teeth and *Pachyrukos*-like jugal and orbit. If the fragmentary specimen is correctly interpreted, derivation of this genus from one with a *Protypotherium*-like jugal would demand a reversion so extraordinary that I cannot believe in its reality, and in that case the genus must either be a derivative of the Hegetotheriidæ with teeth convergent toward the Interatheriidæ, or a phylum independent since the early Tertiary.

[2] In the Santa Cruz, Ameghino described *Icochilus* as differing from *Interatherium* in having premolars of persistent rather than limited growth. Sinclair has shown that *Interatherium*, the older name, was based on specimens with milk teeth.

As has been explained in a previous paper (Simpson, 1932, p. 6), I believe *Plagiarthrus* and *Argyrohyrax* of the *Pyrotherium* Beds to be synonymous and to belong to this family. The lower jaw, type of *Plagiarthrus clivus*, reveals no good generic distinction from *Cochilius*, but it lacks the anterior teeth. The upper dentition, type of *Argyrohyrax proavus*, has very *Cochilius*-like cheek teeth but has I^1–C lower-crowned, with internal cingula, and apparently with lingual enamel. Ameghino placed both those supposed genera in the Archæohyracidæ. Loomis suggested that they might be synonymous, but separated them widely by removing *Argyrohyrax* to the Eutrachytheridæ. In fact both upper and lower teeth are much more like *Cochilius* than they are like either *Archæohyrax* or *Eutrachytherus*. Its more detailed relationships are not clear. If I^1–C are not milk teeth, the genus is distinct and not ancestral to *Cochilius*.

It should be clear from the description above that *Cochilius* is not ancestral to either *Protypotherium* or *Interatherium*, in spite of its close resemblance to both. It has few characters that are not seen in one or the other of the later genera, but such eclectic union of characters confined to one or the other that it can hardly be directly ancestral to either. In the dentition, the lower-crowned anterior teeth and rooted anterior premolars are doubtless primitive. The closed tooth row and unreduced I^2–C are also primitive as well as special resemblances to *Protypotherium*. The median incisors may be somewhat more enlarged than in either, although the difference is slight and variable. The incipient bifurcation of the internal sulcus is also an aberrant character apparently absent in the later genera. The cheek teeth, upper and lower, are otherwise closer to *Interatherium* except that the outer wall of the uppers more resembles *Protypotherium* in the weaker sculpture.

A similar mingling of characters, both primitive and specialized, present in the later genera but not common to both, is seen in the other known parts. On the whole the skull is like that of *Interatherium*, and the lower jaw like that of *Protypotherium*, yet in the placing of the orbit, development of the rostrum, and some other characters the skull is more *Protypotherium*-like. Aside from its slender proportions, the fore limb in general is more like that of *Interatherium* so far as distinctive, especially in the absence of the entepicondylar foramen.

Many of the differences from *Interatherium* and resemblances to *Protypotherium* are primitive characters, and specialized characters tend to indicate the opposite relationship. On this basis, definitely closer affinity with *Interatherium* is indicated. *Protypotherium* is a generally

conservative genus whose ancestry must have diverged from that of *Cochilius* some time before the *Colpodon* Beds were deposited. *Interatherium* is definitely more specialized than *Cochilius*, not directly descended from *C. volvens*, but probably of close common ancestry.

NOTE ON *ARGYROLAGUS*

The genus *Argyrolagus* was described by Ameghino on the basis of a partial lower jaw and considered by him as the last and only known representative of a family of rodents which gave rise to all duplicidentates. Kraglievich (1931) recently redescribed the specimen and opposed its reference to the Rodentia but reached a conclusion still more extraordinary. He believed it to be a marsupial and a true diprotodont, as opposed to the paucituberculates or cænolestoids of South America. He concluded that this implies a connection, direct or indirect, with Australia probably no earlier than the Miocene.

This hinges on the real affinities of *Argyrolagus*. If it is marsupial, then Kraglievich is right in considering it to represent a very distinctive and diprotodont-like family and either, as he supposed, a real diprotodont in a systematic sense or a remarkably convergent type. If it is not marsupial, then the resemblance to the diprotodonts obviously has no more significance than, for instance, the equally marked resemblance of *Pyrotherium* to *Diprotodon*.

The evidence that *Argyrolagus* is a marsupial is essentially the presence of just four molariform teeth, the apparently inflected angle, and the general conformation of the region around and below the base of the coronoid process.

Neither Ameghino nor Kraglievich seems to have considered a third possibility, which is, I believe, the true interpretation of *Argyrolagus:* that it is an aberrant typothere. The presence of four molariform teeth is not remarkable, since most South American ungulates, including the typothere, had long since acquired molariform posterior premolars. The rodent-like incisor and the reduction of the intermediate teeth represent the further development of tendencies often displayed in the Typotheria. The details of *Argyrolagus* in this respect make it a fully distinctive genus of an aberrant phylum, but are not otherwise remarkable for a typothere. The actual shape of the molars, again not exactly like any other typothere genus, is likewise clearly within the potentialities of the group. The molar form is distinctly more typothere-like than it is like any known marsupial.

If some specimens of *Cochilius* were broken in just the same way as is the type of *Argyrolagus palmeri*, they would show an apparently in-

flected angular process and otherwise be just as marsupial-like in this region as is *Argyrolagus*. This fact seems to remove any possible basis for using these characters as evidence of marsupial affinities and to support the other evidence that the genus is an aberrant typothere.

Finally, interesting as it is, there is nothing extraordinary or contrary to other phylogenetic, faunal, and palæogeographic evidence in the development of such a form among the native South American Typotheria, while the presence of a marsupial with these characters at this time and in this place would be so contrary to the probabilities established on such evidence that it could not reasonably be maintained except in the presence of positive proof and in the absence of any acceptable alternative.

The broader, palæogeographic, aspects of Kraglievich's note cannot be discussed at length here, except to point out that it seems beyond question that South America has had no connection with Australia (or with Africa)[1] at least since the Paleocene. There is considerable evidence both for and against an earlier connection, in the Cretaceous or Paleocene, with Australia and, or, Africa, a question not yet susceptible of positive proof one way or another, although I believe the probabilities to be against the reality of either bridge as a migratory route for mammals. But even if these bridges ever did exist, that they disappeared long before the Miocene is as nearly proven as a negative statement can be.

REFERENCES

AMEGHINO, F. 1897. Mammifères crétacés de l'Argentine. (Deuxième contribution à la connaissance de la faune mammalogique des couches à *Pyrotherium*). Bol. Inst. Geog. Arg., XVIII, pp. 406–429, 431–531. [*Archæophylus.*]

1902. Première contribution à la connaissance de la faune mammalogique des couches à *Colpodon*. Bol. Acad. Nac. Ci. Córdoba, XVII, pp. 71–138. [*Cochilius.*]

KRAGLIEVICH, L. 1931. Cuatro notas paleontológicas. (Sobre "*Octomylodon aversus*" Amegh., "*Argyrolagus Palmeri*" Amegh., "*Tetrastylus montanus*" Amegh., y "*Muñizia paranensis*" n. gen., n. sp.). Physis, X, pp. 242–266.

LOOMIS, F. B. 1914. The Deseado Formation of Patagonia. Amherst, Mass.

SIMPSON, G. G. 1932. New or Little-known Ungulates from the *Pyrotherium* and *Colpodon* Beds of Patagonia. Amer. Mus. Novitates, No. 576.

SINCLAIR, W. J. 1909. Typotheria of the Santa Cruz Beds. Repts. Princeton Univ. Exp. Patagonia, VI, pp. 1–110.

[1]Stromer has recently described under the name *Palæothentoides* a supposed cænolestid from the Pliocene of Africa, but its resemblances to the cænolestids are not very close and even its marsupial affinities are still open to some question. It might be an aberrant insectivore, and more material, showing at least the upper teeth, is essential before the occurrence can be considered more than suggestive.